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PHOTOSYNTHETIC PRODUCTION OF THE MACROALGAE *SARGASSUM* AND THE SEAGRASS *ENHALUS*

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ABSTRACT

The rates of photosynthetic production and respiration of the seagrass *Enhalus* and the macroalga *Sargassum*, obtained from a reef flat off Pulau Hantu, an island south of mainland Singapore, were studied *in situ* using an automated respirometer. Oxygen exchange rates were measured at a depth of 3.4m, which yielded instantaneous maximum gross photosynthetic [$Pm_{(gross)}$] rates of 28.41 and 48.33$\mu molO_2chm^{-1}min^{-1}$ for *Enhalus* and *Sargassum* respectively. Respiration rates were low; at 2.57 and 3.43$\mu molO_2chm^{-1}min^{-1}$, the respiratory demands of these species were only 8.30% and 6.67% of their $Pm_{(gross)}$ respectively. Photosynthesis-irradiance (PI) curves were generated for each sample, from which the photokinetic parameters [$Pm_{(gross)}$, Rd and Ik] were estimated. Instantaneous photosynthesis to respiration [$Pm_{(gross)}$/Rd] ratios were 11.05 and 14.09, which were between two to three times larger in magnitude than those obtained for scleractinian corals. Twenty-four hour production and respiration rates at 3.4m were estimated by integrating the photokinetic parameters obtained for both specimens over 7 days of light data. Similarly, estimates for 1.4m were obtained by integrating the PI curves against a set of light data obtained over two days at 1.4m.

INTRODUCTION

Seagrasses and macroalgae are amongst the most productive components of reef ecosystems, and together with other photosynthetically active biota, contribute significantly to the reefs positive carbon balance (McRoy and McMillan, 1977). In many coastal tropical habitats, seagrasses are known to form extensive beds, and are recognised to be important in stabilising sediments, thus reducing coastal erosion and siltation of reefs and associated ecosystems. They also serve as nursery grounds and feeding areas for many of the reef fishes, molluscs and crustaceans (Phillips, 1978; Fonseca and Fisher, 1986).

Unlike temperate waters where macroalgae commonly form extensive meadows, some many meters high (e.g., kelp forests), coastal tropical waters seldom experience macroalgae growth in such magnitude. In many instances, macroalgae form a sub-component of other habitats like seagrass beds and coral reefs, and studies have shown that many benthic seaweeds are extremely productive (Blinks, 1955; Kanwisher, 1966; Mann, 1973).

The growth of seagrasses and other photosynthetically active flora and fauna are often characterised by light limitation (Dennison and Alberte, 1982). Light availability is a function of light attenuation, which is influenced by factors like sedimentation and current movements. Coastal waters of Singapore are characterised by high turbidity, resulting in a rapid decline in light with increasing depth. This has severely affected the vertical distribution of macroalgae and especially seagrasses, which are not found beyond depths of 8 m and 5 m respectively.

The macroalga *Sargassum* has a wide distribution along Singapore reefs, with a growth peak during the Northeast monsoon season. The seagrass *Enhalus* occurs on many reef flats but with very patchy distribution. Neither are highly abundant at the study site, with a percentage abundance of 3.3% and 1.9% for *Sargassum* and *Enhalus* respectively (Tun, 1994).

MATERIALS AND METHODS

This study involved the use of an automated respirometer which was deployed *in situ* on the edge of the reef flat at Pulau Hantu. A full description of the respirometer is given by Tun *et al* (this volume). One 24 hour deployment was conducted for each organism, with four replicates per deployment.

Individual plants of *Enhalus* and *Sargassum* were selected from a reef flat west of Pulau Hantu, an island south of mainland Singapore. Shoots of *Enhalus* with five to ten leaf blades each were chosen and collected complete with stems and about 5cm of rhizome. Young *Sargassum* plants, between 20cm to 30cm in height, were selected and harvested from their attachment points. All colonies were secured onto small lead weights using flexible wires. For each deployment, samples of the same species were placed into four of the five chambers, leaving the fifth as a control to measure the activity of the water body.

Each deployment yielded a set of 4,320 records per sample per day, comprising oxygen concentration, irradiance and temperature data. The rate of oxygen consumption or production (photosynthetic rate) was plotted against average light intensity to give a PI (photosynthesis-irradiance) curve for each specimen. The photokinetic parameters ($Pm_{(gross)}$, Rd & Ik; Table 1) were evaluated by fitting a hyperbolic tangent function (Chalker, 1980, 1981) to the data comprising the PI curves. The goodness of fit for the function was assessed using a least square regression of predicted vs observed values (r^2). Additional parameters (Ic, $I_{0.95}$ & ; Table 1) were subsequently obtained from the fitted curves.

Table 1. Description of photokinetic parameters.

PARAMETER	DESCRIPTION
$Pm_{(gross)}$	Maximal rate of gross photosynthetic production at saturating light intensities
Rd	Dark respiration rate
Ik	Sub-saturation light intensity; light intensity at which the initial slope of the PI curve intersects the $Pm_{(gross)}$ value
Ic	Compensation light intensity
$I_{0.95}$	Estimation of the saturation light intensity; 95% of $Pm_{(gross)}$ and is calculated as 1.832 * Ik
α	$Pm_{(gross)}/Ik$

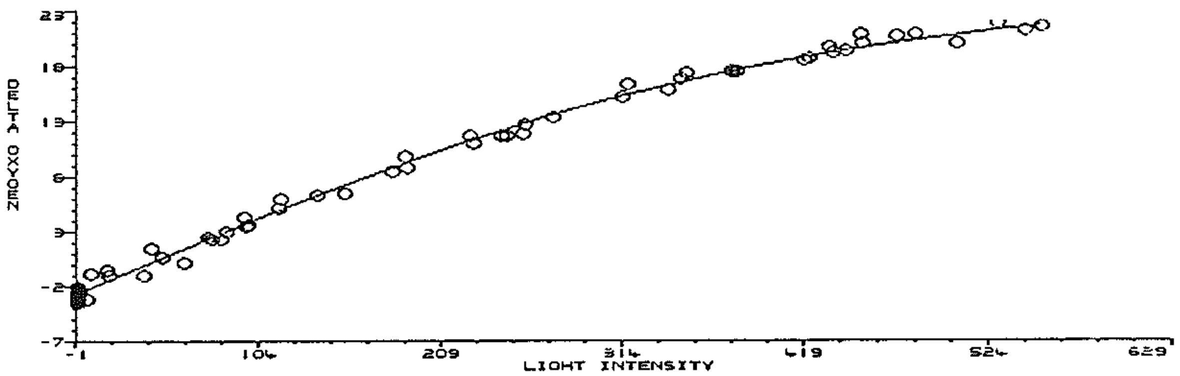
A total of seven days of 24 h light regimes were obtained during the period of these studies, including data from deployments of species not discussed in this paper. Each set of light data was divided into 12 daylight hours (0700 to 1900) and 12 non-daylight hours (1900 to 0700). The PI functions of *Enhalus* and *Sargassum* were integrated over the seven days of light data to give their net and gross 24h production and the total 24h respiration. These calculations included corrections for the volume of each sample, its surface area and the activity of the water body, which was determined from the control chambers.

After each deployment, specimens were taken back to the laboratory and kept frozen at -20C. Following the field work, the organisms were thawed and their volume and surface area of the organisms were determined in litres and cm^2 respectively. The surface area was determined using an area scannner (model Delta-T devices).

RESULTS AND DISCUSSION

The PI responses of one specimen each of *Enhalus* and *Sargassum* are shown in Figures 1 and 2 respectively. All specimens show clearly defined PI responses, with average r^2 values of 0.992 and 0.998 respectively for *Enhalus* and *Sargassum*. Instantaneous $Pm_{(gross)}/Rd$ and daily $Pm_{(24)}/Rd_{(24)}$ values were high; they were between two to three times the values for selected scleractinian corals (Tun *et al*, this volume). Values for the scleractinian *Goniopora* and *Heliofungia* are presented in Table 2 for comparison. Net 24 h production (Net24) of *Sargassum* was greater than that of *Enhalus* at both depths calculated (Table 3).

Figure 1. The photosynthesis-irradiance (PI) curve for one specimen of *Enhalus* deployed at a depth of 3.4m. A hyperbolic tangent function has been fitted into the data comprising the curve, with corresponding photokinetic parameters and goodness-of-fit (r^2) values included.

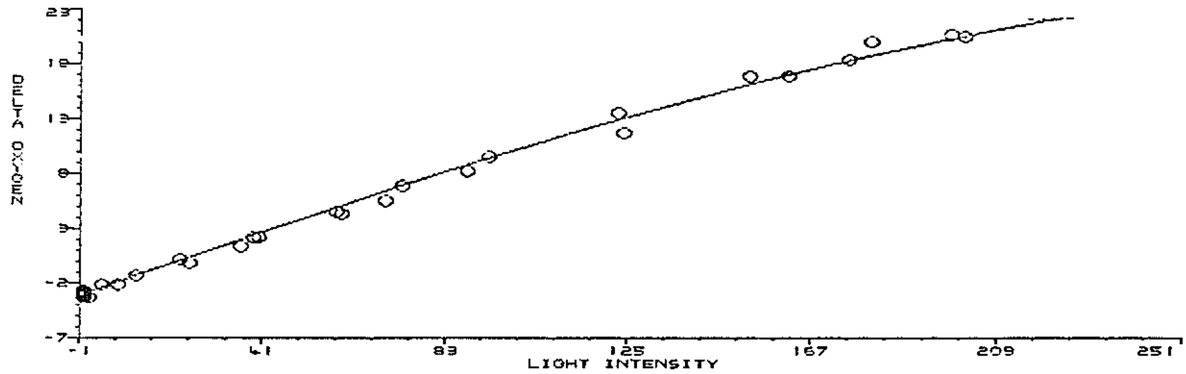


Summary of results for Enhalus :

Deployment run over 1.02 days with 98 time periods.
Model fitted was HYPERBOLIC TANGENT.

Pm	*27.71*	$\mu MolO_2.min^{-1}.chm^{-1}$	*Ik*	*410.41*	$\mu E.m^{-2}.s^{-1}$
Rd	*-2.60*	$\mu MolO_2.min^{-1}.chm^{-1}$	r^2	*0.9965*	

Figure 2. The photosynthesis-irradiance (PI) curve for one specimen of *Sargassum* deployed at a depth of 3.4m. A hyperbolic tangent function has been fitted into the data comprising the curve, with corresponding photokinetic parameters and goodness-of-fit (r^2) values included.



Summary of results for Sargassum :

Deployment run over 1.02 days with 98 time periods.
Mod l fitted was HYPERBOLIC TANGENT.

Pm	*36.36*	$\mu MolO_2.min^{-1}.chm^{-1}$	*Ik*	*262.53*	$\mu E.m^{-2}.s^{-1}$
Rd	*-2.98*	$\mu MolO_2.min^{-1}.chm^{-1}$	r^2	*0.9975*	

The PI relationships for both genera revealed no visible photoinhibition responses (identified by a downturn in the PI curve at elevated light intensities). This is the result of light intensities on the deployment days not having reached level highs enough to invoke photoinhibition. The maximum irradiance during the experiment on *Enhalus* (554µE.$m^{-2}.s^{-1}$) was lower than the estimated saturation light intensity ($I_{0.95}$ =676.61µE.$m^{-2}.s^{-1}$). This was also the case for *Sargassum*.

Seagrasses generally have low photosynthetic rates (Mazzella *et al*, 1979; Dennison and Alberte, 1982, 1985), while some benthic seaweeds appear to be extremely productive (Kanwisher, 1966; Mann, 1973). In this study, the macroalgae *Sargassum* registered a higher production rate [$Pm_{(gross)}$, Pg24 and production efficiency] than the seagrass *Enhalus* (Tables 1 and 2). Average $Pm_{(gross)}$ for *Sargassum* was more than 1.7 times greater than that for *Enhalus* (Table 2), but compared to the two scleractinian genera, their average $Pm_{(gross)}$ were between 4.3 to 7.3 times greater.

The average Ik and $I_{0.95}$ values for *Sargassum* was lower than that for *Enhalus* (Table 2), but was comparable to those for *Heliofungia*. Both genera however, showed considerably lower Ic values than the two scleractinians. *Sargassum* was able to start photosynthesizing at a lower Ic (23.87µE.$m^{-2}.s^{-1}$) and subsequently reach maximum photosynthesis at lower Ik (279.6µE.$m^{-2}.s^{-1}$) or $I_{0.95}$ (512.29µE.$m^{-2}.s^{-1}$) than *Enhalus*. This would enable *Sargassum* to grow at a lower depth than *Enhalus*, where irradiance is reduced. A visual observation confirmed this; growth and distribution of *Enhalus* was limited to reef-flats, but *Sargassum* was still observed along the reef slope. This would also mean that on days when daytime irradiances are low (monsoonal rain, cloud cover, etc.), *Sargassum* would be able to maintain a higher photosynthetic production than *Enhalus* are other scleractinians.

Alpha (α) is calculated as $Pm_{(gross)}$/Ik, and is a measure of the initial slope of the PI curve. A higher value indicates a steeper slope, and thus, greater rates of photosynthesis at sub-saturating light intensities. Used in conjuction with $Pm_{(gross)}$/Rd ratios, a better description of the photosynthetic efficiency of an organism can be derived. *Sargassum* registered the highest and $Pm_{(gross)}$/Rd values, indicating that it is the more productive of the four genera. The value for *Enhalus* was only slightly greater than that for *Heliofungia*, but its $Pm_{(gross)}$/Rd value was almost three times greater. The higher $Pm_{(gross)}$/Rd makes up for the similar, resulting in greater overall production efficiency at a depth of 1.4m (Table 3). On a 24 h basis, an almost three fold reduction was observed in the $Pg_{(24)}/Rd_{(24)}$ ratios, as compared to the corresponding $Pm_{(gross)}$/Rd ratios (Table 2). This was not much lower than the reductions registered by *Goniopora* or *Heliofungia* (between 3 to 5 times reduction).

Table 2. Estimates of the photokinetic parameters (averaged within species; with standard error (SE)) measured at a depth of 3.4m (reef-edge). Units of measurement are; $Pm_{(net)}$, $Pm_{(gross)}$ and Rd (µMolO_2.$cm^{-2}.h^{-1}$), Ik, Ic and $I_{0.95}$ (µE.$m^{-2}.s^{-1}$) and α ([µMolO_2.$cm^{-2}.h^{-1}$]/[µE.$m^{-2}.s^{-1}$]). $Pm_{(gross)}$/Rd and Pg24/Rd24 are unitless. Estimates for two scleractinian corals are included for comparison.

Genera	$Pm_{(gross)}$	Rd	Ik	Ic	$I_{0.95}$	α	$Pm_{(gross)}$/Rd (instantaneous)	Pg24/Rd24 (daily)
Enhalus	28.41	2.57	369.33	35.89	676.61	0.08	11.05	2.62
	(6.23)	(0.82)	(65.06)	(6.13)	(119.20)	(0.03)	(1.92)	(0.58)
Sargassum	48.33	3.43	279.63	23.87	512.29	0.18	14.09	3.65
	(17.03)	(0.84)	(19.46)	(1.26)	(35.64)	(0.07)	(1.54)	(0.27)
Goniopora	6.60	1.30	467.60	96.80	856.60	0.01	5.08	1.03
	(1.30)	(0.11)	(14.40)	(11.10)	(26.30)	(0.00)	(0.6)	(0.25)
Heliofungia	13.80	3.00	267.60	73.50	490.30	0.05	4.60	1.24
	(3.30)	(0.25)	(16.20)	(13.40)	(29.60)	(0.01)	(0.70)	(0.45)

At a depth of 1.4 m, net 24 h production of *Enhalus* and *Sargassum* were 3.73 and 14.55µMolO_2.$cm^{-2}.d^{-1}$ respectively (Table 3). Assuming a respiratory quotient of 1.0, production efficiencies of the two genera were high; at 262% and 365%, they were between 2 to 3 times more productive than the scleractinians *Goniopora* or *Heliofungia* (148% and 130% respectively). A reduction in depth of just 2m (at 3.4m) saw a sudden reduction in the photosynthetic efficiencies of *Enhalus* (50.0% reduction) and *Sargassum* (45.5% reduction); this was not observed for *Goniopora* or *Heliofungia*, which registered reductions in photosynthetic efficiencies of 4.6% and 0.8% respectively. *Sargassum* and *Enhalus*, being autotrophs, depend entirely on photosynthesis for their carbon source. Singapore coastal waters are highly turbid, resulting in a sharp decline in irradiance with increasing depth. Light attenuation measured at the study site was determined as 0.47, which was much higher than the value of 0.08 obtained on the Great Barrier Reef (Cheshire and

Wilkinson, 1991). This rapid attenuation in light would result in a rapid decrease in the photosynthetic productions of both *Sargassum* and *Enhalus*. The scleractinians on the other hand, exhibit a polytrophic mode of nutrition (Johannes, 1974). At depths where irradiance is too low for the zooxanthellae to provide for their daily carbon requirement, they are able to feed heterotrophically to meet their requirement.

For the period of this study, light intensities for the major part of the day were above the compensation points but below the estimated saturating light intensities for all 4 genera. The average of seven days of daylight irradiance was $220\mu E.m^{-1}.s^{-1}$, while the average daytime maximum irradiance was $552\mu E.m^{-2}.s^{-1}$ and the maximum irradiance on any day was $682\mu E.m^{-2}.s^{-1}$.

Table 3. Estimated 24 hour production and respiration, obtained by integrating the photokinetic parameters obtained for individual specimens over the seven days of light data. Average rates for the specimens at two different depths, 3.4m (reef-edge) and 1.4m (reef-flat), are presented. Values for two scleractinian corals are included for comparison. Units of measurement for Net24, Rd24 and Pg24 are $\mu MolO_2.cm^{-2}.d^{-1}$.

Genera	Net 24 h production (Net24)	Total respiration (Rd24)	Gross 24 h production (Pg24)	Production efficiency %; Pg24/(-Rd24)	Depth[1] (m)
Enhalus	0.71	-2.30	3.01	131	3.4
Sargassum	5.43	-5.48	10.91	199	3.4
Goniopora	0.05	-1.81	1.86	103	3.4
Heliofungia	1.05	-4.37	5.41	124	3.4
Enhalus	3.73	-2.30	6.03	262	1.4
Sargassum	14.55	-5.48	20.03	365	1.4
Goniopora	0.74	-1.81	6.46	108	1.4
Heliofungia	2.10	-4.37	1.50	125	1.4

([1]As deployments for the above four genera were carried out at 3.4m, estimates at 1.4m were obtained by integrating their PI curves against a set of light data obtained over two days at 1.4m, from deployments of other specimens not detailed in this paper).

This study represents a preliminary investigation into the productivity of reef organisms on Singapore reefs. The data obtained for this study are comparable to other productivity studies conducted in other parts of the tropics.

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